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PHYLOGENETIC-TAXONOMIC SIGNIFICANCE OF LAST INSTAR OF *PROTOXAEA GLORIOSA* FOX, WITH DESCRIPTIONS OF FIRST AND LAST INSTARS (HYMENOPTERA: APOIDEA)

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Abstract The first and last larval instars of the oxaeine *Protoxaea gloriosa* Fox are described taxonomically. The last stage larva is very different from those of other Andrenidae, a fact suggesting that the Oxaeinae should be elevated to family rank. Certain similarities between *Protoxaea gloriosa* and the *Nomada*-like parasitic authophorids are also noted but are considered to be a result of convergent evolution.

Of the four subfamilies of the Andrenidae, the larval representatives of only the Panurginae and Andreninae have been studied critically to date. The following descriptions of the first and last instars of *Protoxaea gloriosa* Fox are offered here as the first taxonomic account of the immature stages of a member of the third subfamily, the Oxaeinae. The larva of the monotypic South American Euherbstiinae (Moure, 1950) remains unknown. The Oxaeinae, primarily Neotropical in distribution, consist of only two genera, *Oxaea* and *Protoxaea*, with *P. gloriosa* being the most commonly encountered species in the United States. Details of its biology will be presented in a forthcoming paper by Doctors M. A. Cazier and E. G. Linsley

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to whom I am indebted for the specimens described here. The larvae employed in this paper and the intermediate instars are deposited in the collection of the American Museum of Natural History.

In view of the rather close agreement between the mature larvae of the Andreninae (*Andrena*) and those of the Panurginae (to be elucidated in a forthcoming paper), it might have been predicted that the Oxaeinae would also have similar-appearing larvae. As the following discussion reveals, such is not the case. The last stage larva of *P. gloriosa* is remarkably distinct from those of other andrenids and can be distinguished from them on the basis of the following: head capsule darkly pigmented; posterior tentorial pit situated below hypostomal ridge and posterior thickening of head capsule; epistomal ridge well developed along its entire length (in the Andreninae and Panurginae the ridge is usually absent mesiad of the anterior tentorial pits; however, in the panurgine *Panurginus potentillae* (Crawford) it is weakly developed between the pits); parietal band well developed; vertex nonprotuberant (this is also true of the larvae of the panurgine genus *Perdita*, but in view of the other dissimilarities between the larvae of *Perdita* and *Protoxaea*, this condition almost certainly evolved independently in each group); antenna not arising from prominence (in *Perdita* the antennal prominences are very low, but the above parenthetical remark also applies here); labrum cleft apically; mandible long; mandibular apex blade-like and elongate; mandibular base extremely broad as seen in adoral view; labiomaxillary region greatly reduced, fused and recessed; body without dorsal tubercles; spiracles located on pigmented sclerites; atrial wall provided with elongate spines; primary tracheal opening slit-like; and subatrium partly pigmented.

Not only are some of these characters different from those of other mature andrenid larvae, but they are, I believe, unique for bee larvae in general: labrum cleft apically; extreme degree of recession of labiomaxillary region; mandible long and with elongate, blade-like apex; and slit-like primary tracheal opening. The first two features and the long mandibles are also characteristic of the first instar, but the blade-like mandibular apex apparently develops gradually from the more normal mandible of the first instar. What seems to be a third instar possesses elongate-oval primary tracheal openings, a condition intermediate between that of the first and last larval instar.

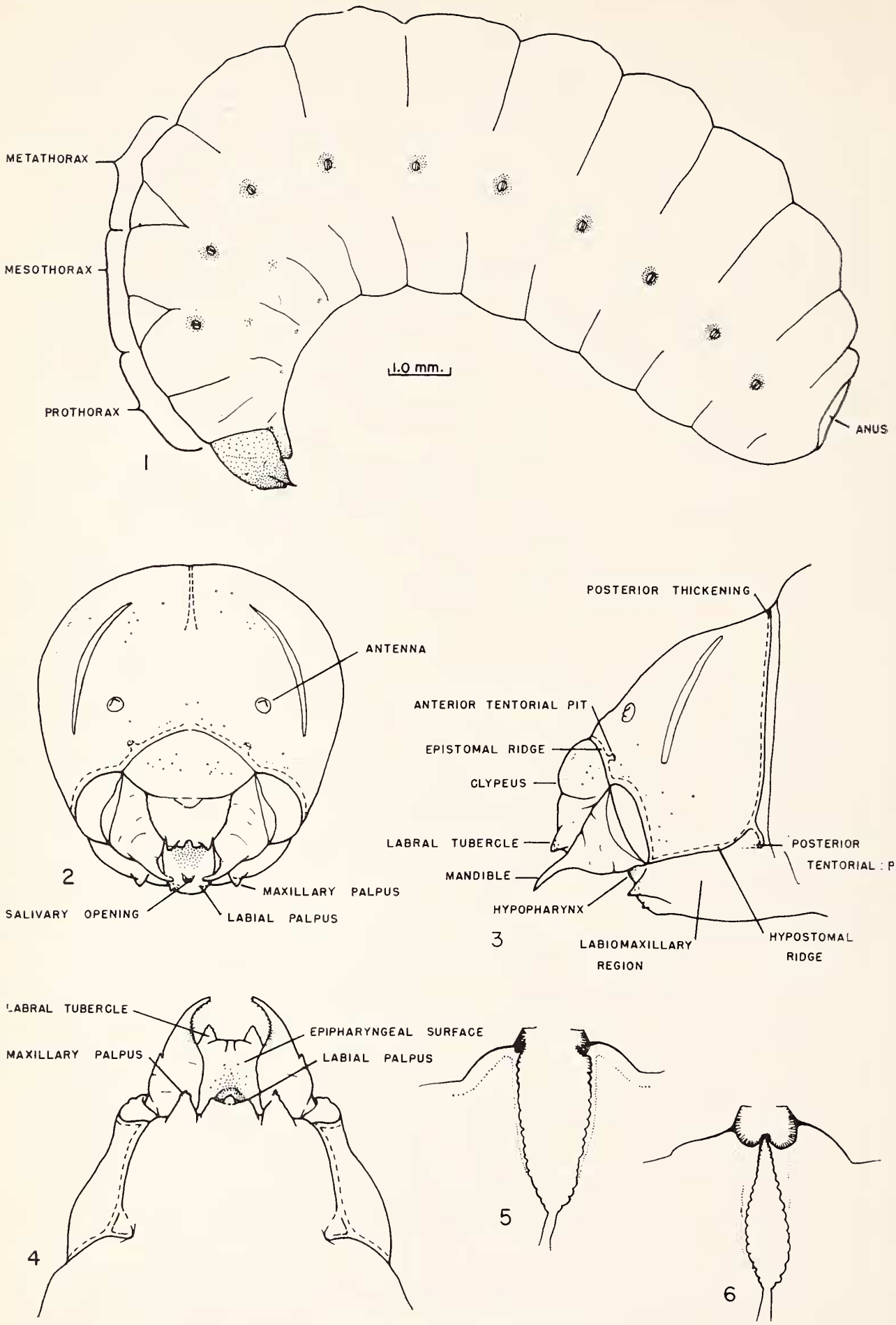
The mature larvae of *P. gloriosa* share the following characters with the other two andrenid subfamilies: antennal papilla low; labral tubercles two; mandible simple apically; maxillary palpus larger than labial palpus; salivary opening a curved slit; body without numerous setae; integument of postcephalic region rigid in hibernating form; peritreme present; and anus situated apically and abdominal segments 9 and 10 otherwise normal. Because larvae with these features are also found in the Colletidae, in the

Halictidae, in the *Nomada*-like parasitic anthophorids, and to some extent in the Melittidae, such characteristics are obviously of little value in determining relationships within the Andrenidae.

To further emphasize the distinctness of the Oxaeinae, it is perhaps important to mention that the mature larvae of the Andreninae and Panurginae share no characters with the Oxaeinae that they do not also hold in common.

In summary then, the mature larva of *P. gloriosa* is markedly different from those of the Andreninae and Panurginae, which resemble each other to a considerable extent. It seems unlikely that other oxaeine larvae, when found, will bridge the gap between this subfamily and the other two, because of the small number of Oxaeinae and because of the pronounced homogeneity of the adults. We must search elsewhere, therefore, for possible intermediate forms. As reported by Michener (1944), the adults of the Old World panurgine genus *Melitturga* share a number of characters with the oxaeines but the male genitalia (Rozen, 1951) of the two groups do not support this implied relationship. A comparison of the larva of *Melitturga* with that of *Protoxaea* may well solve this seeming paradox. However, unless the larva of *Melitturga* fills the hiatus between larval oxaeines and panurgines, it is my opinion that the Oxaeinae should be elevated to family rank because of the combined distinctiveness of the larval and imago stages. If the status of the oxaeines is elevated, their relationships with the colletid Stenotritinae might well be reviewed at the same time.

The similarities between the mature larva of *P. gloriosa* and those of the *Nomada*-like parasitic anthophorids (*Nomada, Triepeolus, Oreopasites,* etc.) are difficult to explain. Not only do the larvae of these two groups share the generalized features also encountered in the Colletidae, Andrenidae, Halictidae, and Melittidae, but they both also exhibit certain specialized characteristics, namely, the peculiar position of the posterior tentorial pits and the absence of antennal prominences and vertexal protuberances. Although, with the mature larvae, the long mandible of *P. gloriosa* contrasts with the short mandible of the parasitic bee, the long mandible of the first instar of *P. gloriosa* is somewhat similar to the extremely long mandible of the first stage parasitic forms. The mature larva of *P. gloriosa* is especially similar to that of *Triepeolus* sp. (I have examined the same series used by Michener, 1953). In addition to the characters referred to above, these taxa share: spiculated hypopharynx; attenuate mandibular apexes (though not blade-like in *Triepeolus* sp.); body without tubercles; spiracles on pigmented, sclerotized plates; and long atrial spines. Presumably the similarities result from convergent evolution, for the adults of Oxaeinae and the *Nomada*-like bees are too dissimilar to suggest a close relationship. The following characters of the last stage larva of *P. gloriosa* are not possessed by the parasitic forms: darkly pigmented head capsule; well-developed parietal



Protoxaea gloriosa Fox

Fig. 1. Live, postdefecating larva, lateral view. Figs. 2–4. Head of postdefecating larva, front view, lateral view, and ventral view, respectively. Figs. 5–6. Optical section of spiracle of postdefecating larva, anterior or posterior view and dorsal or ventral view, respectively. Scale refers to figure 1.

bands; well-developed epistomal ridge; labral cleft; blade-like mandibles; body form not tapering posteriorly.

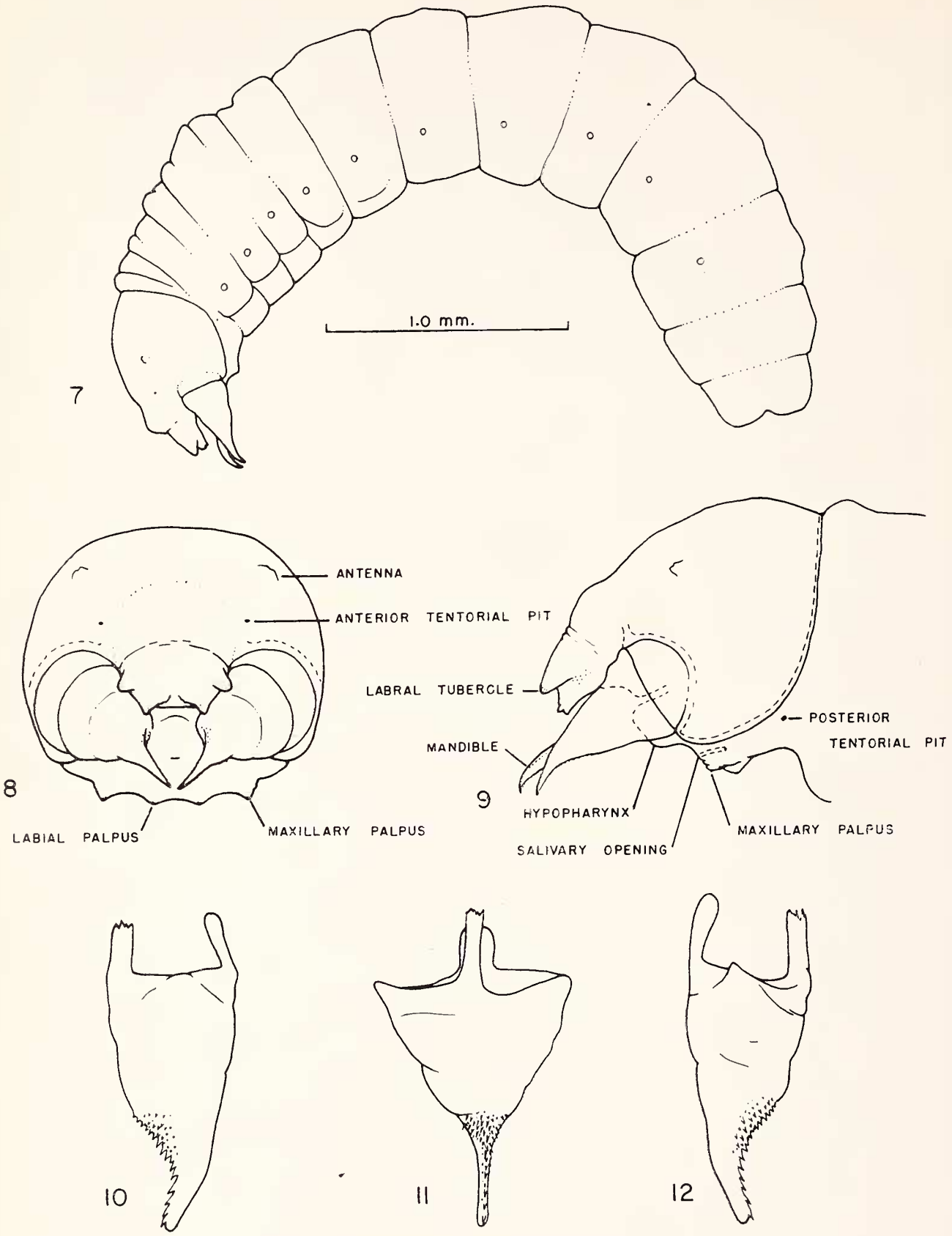
After consuming the provisions, the mature larva defecates and then enters a quiescent, hibernating stage. The following description refers primarily to this quiescent form.

Taxonomic Description of Postdefecating Larva of *Protoxaea gloriosa* Fox
Figs. 1–6, 10–12

HEAD (figs. 2–4) Integument wrinkled, with scattered sensilla; epipharyngeal surface of labrum and hypopharynx spiculate as in figures; entire head including mandibular corium pigmented; parietal bands, all internal ridges, antennal rings and papillae, apex of labrum, apexes of mandibles, salivary gland opening, and palpi more darkly pigmented than other parts; coronal cleavage line and posterior part of labiomaxillary region less pigmented than other parts. Tentorium complete but weak; anterior and posterior arms darkly pigmented; remainder unpigmented; each posterior tentorial pit lying below juncture of posterior thickening and hypostomal ridge but joined to posterior thickening by spur of former; anterior tentorial pits lying just above epistomal thickening; posterior thickening of head capsule moderately thin and resting slightly anterior to posterior margin of capsule (fig. 3); thickening gradually bending forward immediately above juncture of spur to posterior tentorial pit and joining hypostomal ridge; hypostomal ridges, pleurostomal ridges, and epistomal ridges of about the same thickness as posterior thickening; epistomal ridge briefly interrupted medially; longitudinal thickening of head capsule absent; parietal bands well defined. Vertex nonprotuberant; clypeus somewhat protuberant. Antennae not arising from prominences, small; each papilla small and lower than basal diameter; each antenna bearing numerous (perhaps 7) sensilla. Labrum cleft apically and bearing two tubercles which are beset with sensilla, some of which are on small prominences. Each mandible in adoral view (fig. 11) extremely broad basally but tapering rapidly to very thin, elongate, nearly parallel-sided apex; when seen from above or below (figs. 10, 12), mandible moderately narrow basally and gradually tapering to moderately broad apex; consequently apex of mandible blade-like; extreme apex simple when viewed adorally but, when viewed from above or below, with slender, sharp-pointed tooth on adoral side; adoral apical edge beset with numerous sharp-pointed teeth (this edge seems to be the dorsal inner apical edge); there is no indication of a ventral inner edge); somewhat smaller pointed teeth on both dorsal and ventral surfaces in cuspal region. Labiomaxillary region fused, reduced and recessed, as in figures 3 and 4 so that only notable features are palpi and salivary gland opening; maxillary palpi conspicuous, a little longer than basal diameter, and with some sensilla on small prominences; labial palpi much smaller than maxillary palpi; other sensilla on apex of labium on small prominences; salivary opening a small curved slit partly enclosing a low prominence.

BODY Form (fig. 1) tapering and curving anteriorly to relatively small head; posterior part nearly straight but blunt, due at least in part to somewhat telescoped abdominal segments 8, 9, and 10 (the compression results from the larva's resting on the tip of its abdomen in a vertical cell). Mesothorax and metathorax[1] dorsally divided into cephalic

[1] The segmentation of the thoracic region of bee larvae is difficult to understand because the intersegmental lines are weak and easily confused with intrasegmental lines and because the thoracic and first set of abdominal spiracles seem to have migrated forward. However, the intersegmental lines of *Protoxaea gloriosa* are distinctly pigmented, whereas the dorsal intrasegmental lines are not. This being the case, it is obvious



Protoxaea gloriosa Fox

Fig. 7. Preserved first stage larva, lateral view. Figs. 8–9. Head of same, front view and lateral view, respectively. Figs. 10–12. Left mandible of postdefecating larva, dorsal view, adoral view, and ventral view, respectively. Scale refers to figure 7.

and caudal annulets; other segments not noticeably divided on postdefecating form; tubercles very faint, transverse, presumably on anterior part of caudal annulations on predefecating form. Integument rigid, nonspiculate, finely wrinkled, and yellowish, with intersegmental lines more darkly pigmented.[1] Spiracles (figs. 5, 6) resting on elevated, pigmented sclerites, peritreme flat; atrium projecting above body wall; atrial wall darkly pigmented, beset with numerous hair-like spines, and without rim; primary tracheal opening collared and slit-like, with slit at right angles to long axis of body; collar with numerous short spines; subatrium pigmented just below atrium and near attachment of trachea but with area in between unpigmented; subatrial wall bearing spines immediately below atrium. Except for telescoping, abdominal segments 9 and 10 normal, without protuberances, or ridges; anus a transverse slit located apically.

MATERIAL STUDIED Five postdefecating, quiescent larvae, 1 mile north of Rodeo, Hidalgo Co., New Mexico, Sept. 23, 1963 (M. A. Cazier, M. Mortenson).

First Stage Larva

Figs. 7–9

HEAD (figs. 8, 9) Capsule and mouth parts apparently without setae though sensilla may be present; integument unpigmented except for mandibular apexes. Tentorium complete but very weak; posterior tentorial pits situated below posterior thickening and hypostomal ridge; anterior pits somewhat above epistomal groove; posterior thickening of head capsule well defined, similar in thickness to hypostomal ridge; pleurostomal ridge moderately broad but very weak, scarcely noticeable; epistomal ridge not evident but external groove present; parietal bands apparently absent. Antennae moderately developed, perhaps a little more pronounced than those of mature larva. Labral tubercles large; labral apex cleft; labrum bearing spicules laterally but not apically nor on epipharyngeal surface. Mandibular corium nonspiculate; each mandible simple at apex, elongate, bearing small, sharp-pointed teeth scattered along upper and lower apical edges. Maxillae and labium greatly fused, reduced, and recessed; maxillary palpi evident but short; labral palpi evident but even shorter than those of maxillae; salivary opening a short transverse slit.

BODY Form (fig. 7) elongate, cylindrical, without tubercles but with intrasegmental lines at least anteriorly. (Because only one rather poorly preserved first stage larva was available, I was not able to gain an understanding of the intrasegmental annulations; the illustration of the larva in lateral view is incomplete in the thoracic region.) Integument nonsetose but minutely spiculate. Spiracular atrium not pigmented and not projecting above body wall, without elongate spines though perhaps with very short teeth near primary tracheal opening; peritreme apparently missing; primary tracheal opening not on collar and circular in outline, that is, not transverse as in mature larva; subatrium unpigmented, differing little in appearance from trachea. Abdominal segments 9 and 10 normal, without protuberances or ridges; anus apical.

MATERIAL STUDIED One first stage larva, 1 mile north of Rodeo, Hidalgo Co., New Mexico, Aug. 17, 1963 (M. A. Cazier, E. G. Linsley, and M. Mortenson).

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that the mesothoracic and metathoracic dorsa are each subdivided into a cephalic and a caudal annulation with the cephalic one being the narrower. The fact that the spiracles of the first abdominal segment are slightly anterior to the line separating the metathorax from the first abdominal segment suggests that the two pairs of thoracic spiracles belong to the mesothorax and metathorax even though they too lie anterior to the appropriate inter-segmental lines.

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A MALFORMED OVARY IN THE BEDBUG, *CIMEX LECTULARIUS* LINN. (HETEROPTERA: CIMICIDAE).

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Abstract A malformed left ovary is described, in which the number of ovarioles has become reduced, the left lateral oviduct is absent, and the corresponding seminal receptacle is attached to the right lateral oviduct near the right seminal receptacle.

While doing routine dissections on female *Cimex lectularius*, I discovered the ovarian anomaly described here; in several thousand such dissections, this is the only such anomaly I have seen. The right ovary is normal and consists of the usual seven ovarioles. The outer two of these contain full-term eggs ready to be laid; the two ovarioles median to these contain eggs nearly ripe; and the three innermost ovarioles contain less ripe eggs, the egg in one of these ovarioles showing only early stages of yolk-deposition. The right seminal receptacle is normal and greatly distended with sperm.

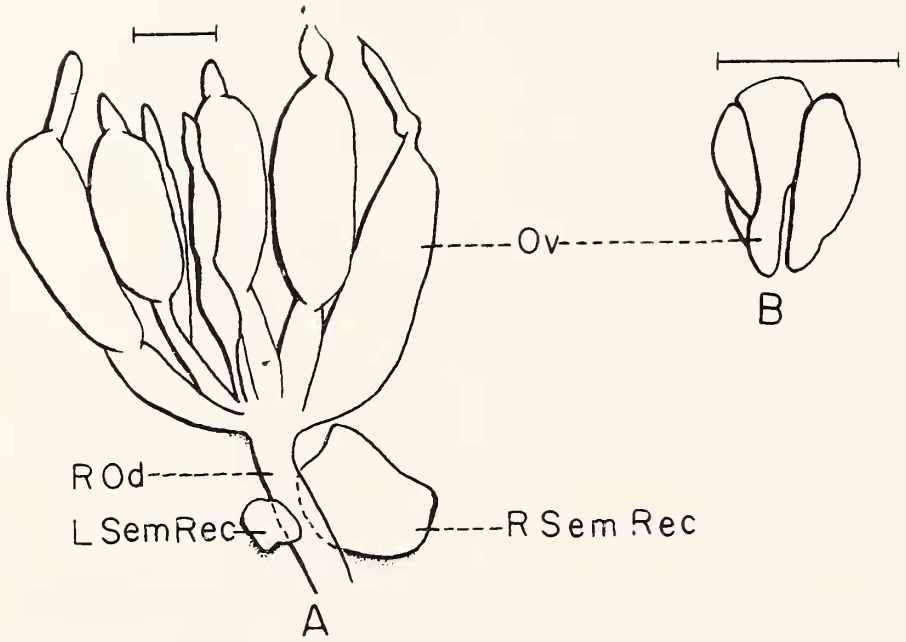

Figure 1. Ovaries of *Cimex lectularius* Linn. A. normal (left). B. anomalous (right). Ov—ovariole, L, R Sem Rec—left, right seminal receptacle; R Od—right oviduct. The scale-markers represent 0.37 mm.